Review of the Bathyal Gastropod Genus *Phanerolepida* (Homalopomatinae) and Description of a New Species from the Oregon Oligocene

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

Two specimens of a new species of *Phanerolepida* Dall, 1907, from separate localities in the middle member of the lower Oligocene Keasey Formation in Oregon, constitute the first record of this deep-water genus outside of Japan and Okinawa. The new species also represents the earliest record of the genus, extending its stratigraphic range back into the Paleogene. It is the purpose of this report to describe the new species, to review the known occurrences of the genus, and to present some hypotheses regarding the evolution, ecological biogeography, and disjunct distribution of the genus.

It is remarkable that a poorly known genus from the Late Tertiary and Recent Japanese deep-water fauna should appear in an early Oligocene deep-water fauna on this side of the Pacific, widely separated in both time and space. *Phanerolepida transenna* (Watson, 1879), the sole living species, is restricted geographically to the area between 33° and 35° N latitude and bathymetrically to muddy substrates in the bathyal (archibenthal) zone, where it is most common between 600 and 800 m (Okutani, 1968). Latitudinal and bathymetric restrictions on the species are further qualified by a unique vertical temperature structure at these latitudes along the Pacific coast of Honshu resulting from the meeting and mixing of the warm surface waters of an offshoot of the Kuroshio current and a submerged offshoot of the cold Oyashio current of Subarctic origin. Thus the temperature between 600 and 800 m in the vicinity of Sagami Bay, where *P. transenna* occurs, is about 6° to 8° C, compared with temperatures in the overlying Kuroshio water averaging 15° C and temperatures in the underlying Western Pacific Bottom Water of 2° to 4° C (Okutani, *op. cit.*). Uda (1937) designates this system between 600 and 800 m as the Intermediate Water, and Okutani (1967, 1968) discusses the characteristics and origin of the bathyal fauna, noting a high proportion of endemic molluscan species with the same restrictions imposed by geography, bathymetry, and water system as *P. transenna*. It is against Okutani's detailed background information on the Recent bathyal fauna of Japan that the significance of the Oregon *Phanerolepida* material can be evaluated.

The TYPE SPECIES in JAPAN

Phanerolepida is characterized by a sturdy turbinate shell of considerably larger size than the small to minute shells of *Homalopoma* Carpenter, 1864. It is further distinguished by a thin, concavo-convex operculum on which the spirals are not externally visible, in contrast to the thick paucispiral external whorl characterizing the operculum of *Homalopoma*. The callus is extensively developed, and in the type species it is divided into a thick portion proximal to the aperture and a thin distal portion through which the underlying ornamentation of the body whorl is visible. The most diagnostic feature of *Phanerolepida* is the net-like, finely-incised rhombohedral pattern of surface sculpture which appears to be unique among the Gastropoda. Both Watson (1879) and Dall (1907) described this surface pattern as having the appearance of shagreen. It is unusual in that the oblique rows of rhombs are not collabral, but inclined in the opposite direction from the aperture and growth lines. The pattern becomes increasingly fine on successive whorls and is sometimes irregularly developed or interrupted by areas of smooth shell deposit.

If *Phanerolepida* were a Recent monotypic genus, one might place less importance on the uniqueness of the net-like surface texture of the shell. However, the pattern now appears to be characteristic not of a single species, but of a lineage that has existed for at least 40 million years. At the same time, the potential for producing a similar but not identical surface pattern apparently exists within the closely related genus *Homalopoma,* as evidenced by its expression in another endemic Japanese species, *Homalopoma granulifera* Nomura & Hatai, 1940. The species occurs in shallow water (less than 100m) along the Japanese coast north of 35° N latitude. Its small size (less than 10mm high), features of the operculum, and the predominance of spiral sculpture are typical of *Homalopoma.* However, a more faintly developed axial sculpture gives the shell a granular appearance. Under magnification the granules exhibit more or less square outlines and either vertical or irregular arrangement (Figure *16*), in contrast to the oblique rows in *Phanerolepida.*

Watson based his original description of *Phanerolepida transenna* on a single live specimen dredged by the *Challenger* from a depth of over 1000m in the Sea of Enshu-Nada (Station 235). He placed his species in the genus *Turbo* Linnaeus, 1758. The original description (Watson, 1879), which was not illustrated, was repeated by Watson (1885-1886) in the *Challenger* Reports, and the holotype was figured.

A second specimen, obtained from deep water in Tokyo Bay by the *Albatross* in 1906 prompted Dall (1907: 168) to propose *Phanerolepida* as a subgenus of *Leptothyra* Pease, 1869. The name is introduced in a discussion at the end of Dall's description of *Basilissa babelica* because the specimen occurred in the same haul with the new species. There are no records indicating that *P. transenna* was collected during the 50 years that followed. Habe (1964: 20) states that the species is "rarely collected from 200 to 500 meters in Sagami Bay."

Okutani (1964) presents the most complete record of *Phanerolepida transenna* in a report based on collections by the R. V. *Soyo-Maru* between 1955 and 1963. He records 10 empty shells and 16 living specimens of *P. transenna* from stations between 550 and 800m in Sagami Bay. Dr. Okutani has graciously provided 7 of these specimens, from 700m in Sagami Bay, for comparison with the new species from the Oregon Oligocene. Two of these specimens have been donated to the U. S. National Museum and are figured in this report (Figures *1, 2, 5, 6, 9,* and *10*).

FOSSIL OCCURRENCES

There are 3 accounts of *Phanerolepida* as a fossil from localities in the Western Pacific. All 3 occurrences are in strata near or above the Miocene-Pliocene boundary, in contrast to the new Oregon species, which comes from strata near the Eocene-Oligocene boundary. Kuroda (1931) described *P. expansilabrum* from the Pliocene of the Nagano prefecture (36°19′N, 138°07′E). Hatai & Nisiyama (1952: 230) consider the age of the strata to be Miocene. I have not seen the holotype, but the spire appears to be higher than in the type species and demarcated by a slightly impressed suture. Kuroda's figure is not good enough to show details of surface pattern. Otuka (1968) documents the occurrence of *P. transenna* from the Pliocene Tomiya sandstone of the Chiba prefecture (35°12′N, 139°51′E). Okutani (1968) discusses the paleoecology of the Tomiya fossil assemblage and cites evidence that it formed under a similar set of environmental restrictions as those found in the vicinity of Sagami Bay. The Recent and fossil occurrences of *Phanerolepida* in Japan are summarized in Figure 17.

One western Pacific occurrence of *Phanerolepida* has been recorded outside of Japan proper. MacNeil (1960:

Plate Explanation

Phanerolepida transenna Watson

Figures *1, 5,* and *9*: USNM 707162. Hypotype. Apertural, top, and side views. Recent, Japan. × 1.5

Figures *2, 6,* and *10*: USNM 707163. Hypotype. Apertural, top, and side views. Recent, Japan. × 1.5

Figure *14*: USNM 707163. Hypotype. a – Detail of surface texture from penultimate whorl. b – Detail of surface texture from body whorl. × 10

Phanerolepida rehderi MacNeil

Figures *3, 7,* and *11*: USNM 562794. Holotype. Apertural, top, and side views. Miocene or Pliocene, Okinawa. × 1.5

Figure *13*: USNM 562795. Topotype. Top view. Miocene or Pliocene, Okinawa. × 1.5

Phanerolepida oregonensis Hickman, spec. nov.

Figures *4, 8,* and *12*: USNM 646902. Holotype. Apertural, top, and side views. Oligocene, Oregon. × 1.5

Figure *15*: USNM 646902. Holotype. Detail of surface texture from body whorl. × 10

Homalopoma granulifera Nomura & Hatai

Figure *16*: ANSP 242880. Hypotype. Detail of surface texture from body whorl. Recent, Japan. × 10

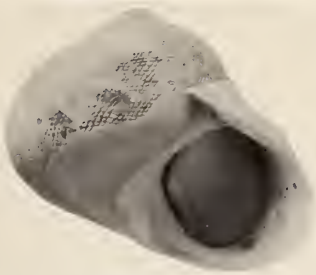

Figure 1

Figure 2

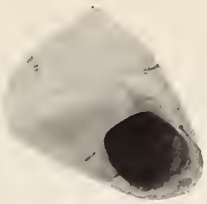

Figure 3

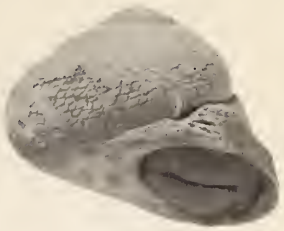

Figure 4

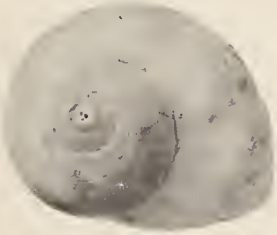

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

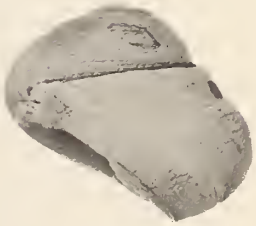

Figure 12

Figure 13

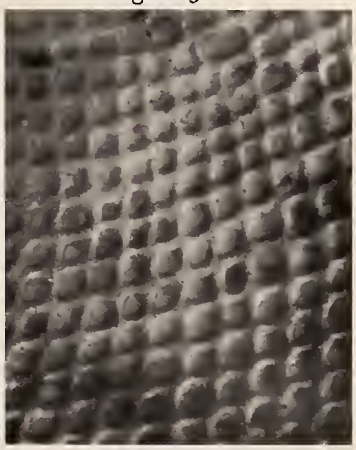

Figure 14 a

Figure 14 b

Figure 15

Figure 16

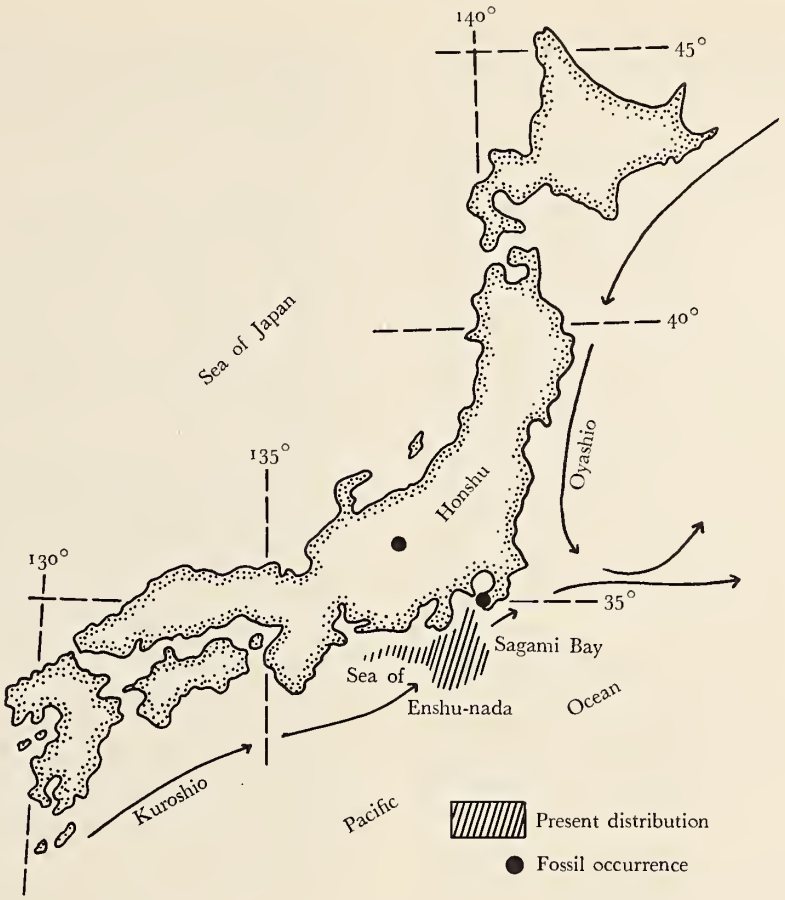

Figure 17

Recent and fossil occurrences of *Phanerolepida* in Japan

30) described *P. rehderi* from beds near the Miocene-Pliocene boundary on Okinawa, at the southern end of the Ryukyu Islands south of Japan. The species is represented by 5 specimens from 2 localities in the Shinzato tuff member of the Shimajiri Formation between 26°05′ and 26°20′N latitude on Okinawa. MacNeil's species has sculpture which is intermediate in coarseness between *P. transenna* and the new species from the Keasey Formation. The shell has a distinctive outline resulting from an abrupt steepening of the apical whorls. Interruption of the reticulate sculpture pattern seems to be more common in *P. rehderi* than in the Recent *P. transenna*. Sharply demarcated areas of unornamented shell are present on the holotype, and on the topotype most of the body whorl lacks reticulate sculpture (Figures *3, 7, 11, 13*).

The Shinzato tuff fauna is a deep-water assemblage which resembles the Keasey fauna in the presence of *Bathybembix* and a diverse component of turrid gastropods. MacNeil (1960: 17) examined depth ranges of living relatives of species in the Shinzato tuff and reported that most occur between 560 and 720 m.

SYSTEMATIC PALEONTOLOGY

Turbinidae

Homalopomatinae

Phanerolepida Dall, 1907

Type, by monotypy, *Turbo transenna* Watson, 1879.

Living, Japan.

Phanerolepida oregonensis Hickman, spec. nov.

(Figures *4, 8, 12*)

Description: Shell large for subfamily, robust, heavy, with 3 whorls on type specimen; apex abraded; aperture circular and nacreous within, prosocline at an angle of about 60° from the axis of coiling; inner lip covered by a broad crescent-shaped callus; suture slightly canaliculate; surface cross-hatched by impressed irregularly spaced spiral and oblique axial lines which divide the surface into small rhombs and give the shell a scaly or net-like appearance. The oblique rows of rhombs are not collabral but inclined in the opposite direction from the aperture and lines of growth. The surface pattern may be interrupted by small areas of shell with faint spiral sculpture, and on early whorls there is faint spiral sculpture superimposed on the rhombohedral sculpture.

Dimensions of Holotype: height 19 mm; maximum diameter 23.2 mm.

Hypotype: height 10.5 mm; maximum diameter 15 mm.

Remarks: *Phanerolepida oregonensis* differs from both *P. transenna* and *P. rehderi* in having a much more strongly prosocline aperture, a more compressed form, and coarser surface sculpture.

Phylogenetic Implications: In the known species of *Phanerolepida,* the rhombohedral surface sculpture has become progressively finer since the beginning of the Oligocene. The hypothesis that coarse sculpture is primitive in the genus is supported by the preservation of coarse sculpture on the early whorls of all species, since it is in accord with the principle that mutations which affect early ontogeny are less often viable than alterations in later stages of development (Figures *1* to *15*).

Origin of *Phanerolepida* from a *Homalopoma*-like ancestor is suggested by the faintly spiral ridges on the early whorls of the Miocene or Pliocene species (Figures *7, 13*) and the superposition of faint spiral sculpture on the rhombohedral sculpture of early whorls in the Oligocene species (Figure *12*). Faint spiral sculpture occurs on the early whorls of some specimens of the Recent species, but it is not discernible on most. There are areas on both the Paleogene and Neogene species where the characteristic reticulate texture is replaced by an apparent relapse of smooth shell deposit marked by faint spiral ridges. One such area occurs on the body whorl of the holotype of *P. oregonensis* (Figure *4*). The term "relapse" seems particularly appropriate with respect to the topotype of *P. rehderi,* on which the reticulate sculpture moves from coarse to fine and back to coarse again before it finally disappears on the body whorl (Figure *13*).

Holotype: U. S. National Museum 646902. Hypotype: USNM 646903.

Occurrences: The holotype was collected by the author in the blue-gray massively bedded siltstone exposed in the abandoned Smithwick-Haydite Quarry on the Spokane, Portland, and Seattle Railroad; NW¼ Sec. 8, T3N, R4W; Vernonia Quadrangle (USGS locality 25031). The type locality falls in the upper part of what has informally been designated as the middle member of the Keasey Formation (Warren & Norbisrath, 1946). Lower Oligocene.

A smaller, poorly-preserved specimen was discovered in a collection made by Harold Vokes in conjunction with the geologic mapping of northwestern Oregon (Warren *et al.,* 1945). The specimen comes from USGS locality 15267, the second large cut from the south end of the high trestle crossing Oregon Highway 47, 1.4 miles due west of Hoffman Hill Lookout, Vernonia Quadrangle. This locality is separated from the type locality by about 5 km. USGS loc. 15267 appears to be slightly lower in the middle member of the formation, although the precise vertical separation cannot be determined because the two localities are on opposite sides of a heavily forested valley and attitudes are too variable in the region for accurate extrapolation.

DISCUSSION

The discovery of *Phanerolepida* in the early Oligocene of western North America raises some interesting questions of historical biogeography and lends new perspective to the question of the pronounced endemism in the Japanese bathyal fauna.

Discussions of endemism in living species have focussed on the distinctions between relict (paleoendemic) and newly evolved (neoendemic) taxa (Stebbins & Major, 1965: 3). *Phanerolepida* is now a relict or paleoendemic genus. It is not clear, however, whether the sole Oligocene occurrence represents a neoendemic phase, nor is it possible to determine whether the genus made its first appearance in the Eastern or Western Pacific.

There are two major possible patterns of distribution for the genus during the Tertiary. It might have been a geographically widespread and broadly adapted member of the bathyal fauna that has declined to a small, highly specialized relict population; or it may have evolved as a specialist and migrated as a small narrowly adapted